RESEARCH ARTICLE

New insights from serranid fishes on the role of trade-offs in suction-feeding diversification

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SUMMARY

Suction feeding is central to prey capture in the vast majority of ray-finned fishes and has been well studied from a detailed, mechanistic perspective. Several major trade-offs are thought to have shaped the diversification of suction-feeding morphology and behavior, and have become well established in the literature. We revisited several of these expectations in a study of prey capture morphology and kinematics in 30 species of serranid fishes, a large, ecologically variable group that exhibits diverse combinations of suction and forward locomotion. We find that: (1) diversity among species in the morphological potential to generate suction changes drastically across the range of attack speeds that species use, with all species that use high-speed attacks having low capacity to generate suction, whereas slow-speed attackers exhibit the full range of suction abilities (this pattern indicates a more complex 'ram–suction continuum' than previously recognized); (2) there is no trade-off between the mechanical advantage of the lower jaw opening lever and the speed of jaw depression, revealing that this simple interpretation of lever mechanics fails to predict kinematic diversity; (3) high-speed attackers show increased cranial excursions, potentially to compensate for a decrease in accuracy; (4) the amount of jaw protrusion is positively related to attack speed, but not suction capacity; and (5) a principal component analysis revealed three significant multivariate axes of kinematic variation among species. Two of the three axes were correlated with the morphological potential to generate suction, indicating important but complex relationships between kinematics and suction potential. These results are consistent with other recent studies that show that trade-offs derived from simple biomechanical models may be less of a constraint on the evolutionary diversification of fish feeding systems than previously thought.

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Key words: suction feeding, ram speed, cranial kinematics, Serranidae, trade-off.

INTRODUCTION

One of the central contributions that physiology and biomechanics have made to evolutionary biology has been to provide an understanding of the trade-offs that shape diversification of functional systems (Shoval et al., 2012). The major axes of functional and ecological diversity within evolutionary radiations are typically thought to reflect the major trade-offs within the functional systems that underlie the diversity. Two trade-offs have often been highlighted as playing a strong role in shaping diversification of the feeding mechanism in ray-finned fishes. First, it is thought that the ability to suction feed trades off with the ability to capture fish by rapid pursuit, often referred to as the 'ram–suction continuum' (Norton and Brainerd, 1993; Wainwright et al., 2001). Second, the fundamental trade-off in levers between the transmission of force and speed is thought to result in readily predicted consequences for kinematic patterns of jaw movement during feeding (Westneat, 1994; Wainwright and Richard, 1995; Westneat, 2004). Although the discussion of these trade-offs is extensive in the literature, there have been fewer attempts to evaluate the empirical distribution of species in the parameter space that should

reveal the trade-offs. Some recent studies have found much greater diversity in trait combinations than expected based on underlying trade-offs (Van Wassenbergh et al., 2007; Holzman et al., 2012b) and generally raise the possibility that in complex systems trade-offs can often be overcome during diversification.

In the present paper we explore several of the expected associations between the morphological design of the feeding system and kinematic patterns in fishes that feed using a combination of suction and forward locomotion during their strike. Our data set is derived from 30 species of Serranidae, a highly successful and diverse group of predatory marine fishes that primarily live on rocky and coral reefs (Randall, 1967; Wainwright and Richard, 1995; Wainwright and Bellwood, 2002). This large sample of relatively closely related species allows us to explore trade-offs and patterns of association between morphology and kinematics within the context of a recent radiation, minimizing major differences between taxa due to phylogenetic distance. We address a series of five issues.

(1) Is the capacity to generate suction pressure associated with the approach strategy of fish attacking their prey? Specifically, do we see a negative association between the capacity to generate

suction pressure, as estimated by the suction index (Carroll, 2004; Collar and Wainwright, 2006) and attack speed, as might be expected from the standpoint of behavioral strategies for prey capture (Norton and Brainerd, 1993; Gibb and Ferry-Graham, 2005) or from a more mechanical perspective (Van Damme and Aerts, 1997; Muller and Osse, 1984)? Some theoretical considerations have yielded the insight that many fast-attacking species are generating considerable suction that, because of the relative motion of predator and prey, is not seen as movement of the prey toward the predator (Muller and Osse, 1984). Further, the translational pressure that fast-attacking species experience means that they do not require as strong suction during prey capture as slow-attacking species. Thus, we may see evidence that high-speed attackers are equally capable of generating suction as low-speed attackers (Van Damme and Aerts, 1997) or that fast-attackers have faster jaw expansion because of the passive assistance of water filling the oral cavity (Muller and Osse, 1984).

Previous observations also led to the idea that moving toward the prey during the strike could be viewed as an alternative to a predator using suction to draw the prey into the mouth; the so-called ram–suction continuum (Norton and Brainerd, 1993). Attempts to quantify the position of species on this continuum have mostly used the ram–suction index (Norton and Brainerd, 1993), which characterizes the relative distance covered by the predator swimming toward the prey during the strike and the distance the prey is drawn into the mouth. However, other work has shown that suction distance shows little variation among species because suction feeders are limited to drawing prey from a maximum of approximately one mouth diameter, whereas attack distances may vary widely (Wainwright et al., 2001; Porter and Motta, 2004; Day et al., 2005). Thus, relative suction performance may be better characterized by the ability to generate strong suction pressure and thus, high flow speeds and accelerations (Wainwright and Day, 2007; Holzman et al., 2008b; Van Wassenbergh and Aerts, 2009). Using the suction index (Carroll et al., 2004), based on morphological measurements as a metric of suction performance, we ask whether a capacity for strong suction characterizes species that use less locomotion when attacking prey.

(2) The mechanical advantage of jaw levers captures a fundamental trade-off between force and velocity transmission of the muscle contractions that are input to the lever (Wainwright and Richard, 1995; Westneat, 2004), but recent work has challenged the straightforward implication of lever mechanical advantage for velocity transmission because lever mechanics inevitably have impacts on muscle mechanics and the interaction may not be easily predicted (McHenry, 2011). Interestingly, there are few comparative data in the literature on fish feeding functional morphology that allow one to empirically evaluate the widely assumed relationship between jaw lever mechanical advantage and the speed of jaw movements. We explore this issue by examining the relationship across species between the mechanical advantage of the jaw depression lever and the speed of mouth opening; this is the first quantitative analysis of this relationship across a large, diverse group of fish. The expectation is that species with a lower mechanical advantage in the jaw depression lever will have faster jaw depression (Westneat, 1994; Wainwright and Richard, 1995).

(3) Do species with a greater attack speed have greater cranial excursions during the strike? Comparisons between two centrarchid species led to the suggestion that greater attack speed is associated with reduced strike accuracy (Higham et al., 2005). Reduced accuracy during a fast-swimming strike may be partly overcome if the species has a larger mouth size when the prey is intercepted (Higham et al., 2007). We examine this relationship by looking at the relationship between attack speed and both maximum gape during the strike and anatomical mouth width; we also expand our comparison beyond mouth size to ask whether other kinematic excursions of the head during the strike are generally greater in species that use higher attack swimming speed.

(4) There are two major benefits of upper-jaw protrusion to suction feeders. Protrusion can be viewed as contributing to attack speed because it increases the speed of the mouth moving toward the prey (Motta, 1984). Protrusion can also significantly increase the hydrodynamic forces that a suction feeder exerts on its prey (Holzman et al., 2008c). Although these benefits of jaw protrusion are not mutually exclusive, we may see different associations across species if strong suction feeders use less approach speed (Question 1 above). We examine this issue in our sample of serranid species and ask whether jaw protrusion is associated with suction index or with attack speed.

(5) How are the kinematics of a strike related to the capacity to generate suction pressure? Few studies have explored how the potential to generate suction relates to kinematics during strike performance. We therefore ask whether the morphology of a species is related to the pattern of jaw and buccal skeleton movement.

To address these questions we collected data from 30 species of Serranidae (Craig and Hastings, 2007; Smith and Craig, 2007) (Table 1). Serranids are an excellent group with which to address the above questions for several reasons. First, serranids are an ecologically diverse family, including piscivores, planktivores and species that feed primarily on benthic invertebrates (Randall, 1967; Wainwright and Richard, 1995), and there is moderate variation among lineages in body and head shape. Second, it has been noted that different serranid species use different strategies to capture prey, including ambush tactics and active pursuit (Randall, 1967; Wainwright and Richard, 1995; Wainwright and Bellwood, 2002). Because their diversity is focused along the 'ram–suction continuum', this group is well suited for explorations of the relationship between jaw mechanics and feeding kinematics, and the 30 species used in this study span the variation in strategies to capture prey, diet, and use of ram and suction used during a strike.

MATERIALS AND METHODS

Wild-caught fish from the Indo-Pacific region were obtained commercially from the aquarium industry and Caribbean species were collected in the Florida Keys. Specimens were brought to the laboratory at the University of California, Davis, and maintained at 22°C in 40 or 110 liter aquaria depending on the size of the fish. We filmed feeding sequences from a total of 72 specimens from 30 species, including 10 species from each of three subfamilies of Serranidae (Craig and Hastings, 2007; Smith and Craig, 2007), the Epinephelinae, Serraninae and Anthiinae (Table 1). Although these three subfamilies are currently recognized as belonging to Serranidae, recent phylogenetic work indicates that they do not make up a monophyletic Serranidae, although the groups are closely allied (Craig and Hastings, 2007).

We filmed feeding events using a NAC Memrecam ci digital system (Tokyo, Japan) high-speed video camera at 500 frames s^{-1} or a Fastec HiSpec 1 system (San Diego, CA, USA) at 1000 frames s^{-1}. Two 120 W halogen lights were placed outside of the aquaria to allow for proper lighting during filming. Fish were starved for at least 24 h prior to filming and fed live zebrafish (*Danio rerio*) or mosquitofish (*Gambusia* sp.) during recording sessions; larvae were used for smaller species, and adults used for larger species. For each individual we analyzed several successful strikes (approximately three to 10), which were characterized by the fish

Table 1. Values for mean (±s.d.) attack speed, strike distance and suction index for each species used in the study

Species	N	Attack speed (mm s⁻¹)	Strike distance (mm)	Suction index[a]
Epinephelinae				
Chromileptes altivelis	2	181.66±39.90	10.29±5.26	0.109±0.016
Epinephelus ongus	4	1245.42±538.22	17.95±8.20	0.044±0.013
Liopropoma carmabi	1	178.53±103.83	4.80±3.18	0.088
Liopropoma eukrines	1	977.61±326.34	11.13±0.90	0.062
Liopropoma mowbrayi	1	971.57±406.14	9.19±2.77	0.059
Liopropoma rubre	3	1223.90±570.95	10.86±4.09	0.047±0.014
Paranthias furcifer	4	357.48±274.49	9.09±4.20	0.140±0.048
Plectropomus maculatus	3	1212.70±475.31	17.89±5.37	0.057±0.011
Rypticus maculatus	2	208.58±68.41	6.15±1.77	0.052±0.008
Variola louti	1	399.11±357.85	9.07±2.53	0.056
Serraninae				
Diplectrum formosum	1	428.09±122.85	9.13±6.12	0.045
Hypoplectrus puella	2	360.07±246.50	12.34±5.52	0.162±0.066
Hypoplectrus unicolor	2	230.03±182.53	10.19±4.97	0.244±0.003
Serranus annularis	3	521.30±446.90	5.08±3.39	0.023±0.003
Serranus baldwini	3	423.60±233.44	4.82±3.33	0.022±0.006
Serranus chionaria	3	140.33±72.62	3.45±2.43	0.049±0.014
Serranus phoebe	1	232.68±89.77	3.99±4.48	0.089
Serranus tigrinus	3	338.46±106.53	7.90±3.21	0.047±0.005
Serranus tobacarius	3	1239.83±521.47	16.16±4.59	0.045±0.003
Serranus tortugarum	3	605.05±322.43	9.78±3.69	0.138±0.036
Anthiinae				
Odontanthias borbonius	1	128.33±45.76	2.73±4.11	0.573
Plectranthias inermis	1	1277.88±508.82	11.71±3.03	0.058
Pseudanthias bartlettorum	4	387.45±205.72	5.92±2.66	0.077±0.042
Pseudanthias dispar	1	318.09±47.27	6.45±0.80	0.090
Pseudanthias evansi	3	213.74±59.39	3.68±1.45	0.081±0.003
Pseudanthias fasciatus	4	411.23±207.25	8.00±4.44	0.190±0.039
Pseudanthias hutchii	1	305.08±69.35	6.69±4.16	0.106
Pseudanthias pleurotaenia	3	303.14±153.28	6.31±1.47	0.351±0.143
Pseudanthias squamipinnis	5	247.73±141.45	4.41±2.85	0.206±0.114
Serranochirrhitus latus	2	189.49±90.31	3.65±1.55	0.339±0.039

For a complete list of all kinematic and morphological mean trait values for each species, see supplementary material Tables S1, S2.

[a]Standard deviations were calculated on individuals; therefore, species with N=1 do not have a standard deviation. Note that for kinematic traits, standard deviations were calculated based on three strikes per individual per species, which allows for a single individual to have a standard deviation.

appearing to be oriented perpendicular to the camera and in focus (Fig. 1). All fish were filmed in their housing tanks, and after each feeding trial a ruler was filmed to scale the images.

We then tracked 11 landmarks (see supplementary material Fig. S1) through each feeding sequence using a custom modified version of the DLTdv3 package for MATLAB (Hedrick, 2008; Holzman et al., 2012a). In short, point 1 represents the anterior tip of the upper jaw, point 2 represents the anterior tip of the lower jaw, point 3 is a dorsal and point 4 a ventral body point behind the operculum, point 5 is the estimated center of mass of the prey, point 6 is an earthbound reference, point 7 is an anterior point along the lower jaw, point 8 a posterior point along the lower jaw, point 9 is a ventral point on the head anterior to the operculum and above the hyoid, point 10 is a dorsal point on the head anterior to the operculum and point 11 is the ventral-most appearance of hyoid complex.

We used these 11 landmarks to derive several kinematic variables during a strike (supplementary material Fig. S1, Table S1). We measured times with reference to the time of 20% of peak gape and defined peak gape at 95% of peak gape because of the asymptotic relationship that gape usually displays at onset and maximum expansion. Gape was the distance between the anterior tip of the premaxilla (point 1) and anterior tip of the lower jaw (point 2). Jaw protrusion was the displacement of the center of a line between points 1 and 2 in relation to the head (point 9), a measure of how much the mouth extends. Hyoid depression was the displacement of the

hyoid bone (point 11) in relation to the head (point 9). Lower jaw rotation was the angle of the lower jaw (points 7 and 8) relative to the skull (points 9 and 10). Cranial rotation was the angle between the head (points 9 and 10) and the body (points 3 and 4) as the head rotates during the strike. Finally, strike distance was the distance from the center of a line between points 1 and 2 (position of the mouth) to the prey (point 5) at the time when the mouth was at 20% peak gape. We also obtained the timing for all of these variables, except strike distance; instead, we obtained time to prey capture, which is the time it takes for the prey item to cross the line from points 1 and 2 starting at 20% peak gape. Therefore, for each cranial excursion, we obtained the maximum excursion and the time to reach the maximum value. Based on the timings we obtained the mean speeds of the excursions; for maximum gape and jaw protrusion, speeds were expressed as millimeters per second, whereas for maximum lower jaw and cranial rotation, speeds were expressed as degrees per second. Finally, we obtained attack speed during the strike in millimeters per second (20–95% peak gape).

A total of 636 videos were digitized from 72 individual fish. For each individual we calculated means for all kinematic variables from the sequences corresponding to the shortest three times to peak gape sequences, this was thus a measure of mean maximum performance. This resulted in a truncated data set based on 216 feeding sequences, on which all further analyses were performed. All traits were log₁₀-transformed and corrected for body size by calculating residuals

A **B**

Strike initiation:
20% peak gape
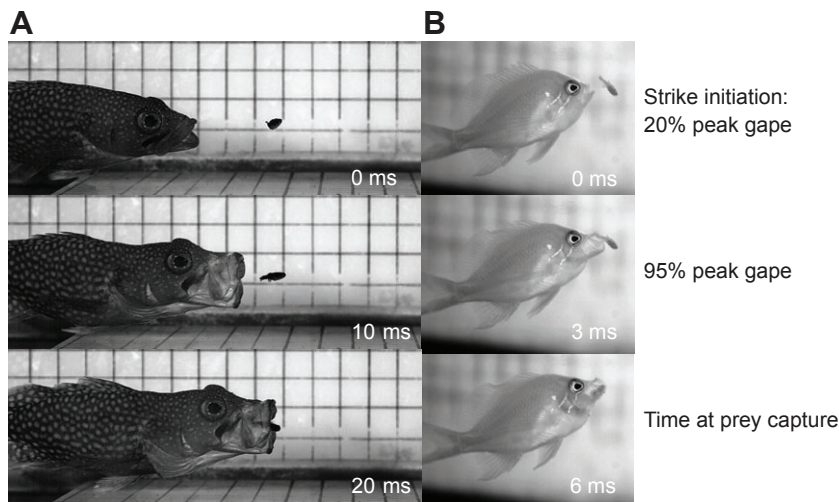
95% peak gape

Time at prey capture

Fig. 1. Representative kinematic sequences of (A) *Epinephelus ongus*, a species that exhibits longer strike distances, high attack speed and low suction index, and (B) *Serranocirrhitus latus*, a species on the other end of the ram–suction continuum with short strike distances, low attack speed and high suction index. Images not to scale.

from regressions with $\log_{10}$ standard length, if the trait was significantly related to size. All traits were significantly related to size, except attack speed, cranial rotation and lower jaw rotation.

After filming, each fish was euthanized with a lethal dose of MS-222, preserved in formalin, and at a later date cleared and stained for bone and cartilage (Taylor and Van Dyke, 1985). Using cleared and stained specimens, we measured two mechanical systems in the feeding apparatus, the lower jaw opening lever (Wainwright and Richard, 1995) and the suction index (Carroll et al., 2004) (supplementary material Table S2). For the former we measured the in lever of the lower jaw opening system from the middle of the articular-quadrate joint to the insertion site of the interoperculo-mandibular ligament on the mandible. The out-lever of the lower jaw opening was measured from the center of the jaw joint to the most anterior tooth row. The mechanical advantage of the lower jaw opening system was measured as the ratio of the in-lever to the out-lever.

Suction index was calculated following previous studies (Carroll, 2004; Collar and Wainwright, 2006; Holzman et al., 2011; Holzman et al., 2012b) using the following formula:

$$\text{Suction index} = \frac{A_E \times \left(\dfrac{L_{in}}{L_{out}} \right)}{L_{buccal} \times d_{mouth}} \, , \quad (1)$$

where L_{in} is the length of the in-lever for the epaxial muscles, L_{out} is the out-lever for the force owing to the buccal pressure drop, A_E is the cross-sectional area of the epaxial muscles, L_{buccal} is the buccal length, d_{mouth} is the mouth diameter and $L_{buccal} \times d_{mouth}$ gives the projected area of the buccal cavity (Carroll et al., 2004). Specifically, L_{in} is the moment arm of the epaxial muscle and was measured from the joint between the post-temporal and supracleithrum to the centroid of the epaxial muscle cross-section; L_{out} is the distance from the post-temporal/supracleithrum joint to the area of moment of the projected buccal area, and was measured as half the length of the buccal cavity plus the distance from the posterior edge of the buccal cavity to the post-temporal/supracleithrum joint. Mouth diameter was measured as the width of the mouth on cleared and stained specimens. Finally, A_E was calculated based on the area of an ellipse from the height and width of the epaxial muscle. Suction index, which was developed with species of Centrarchidae, and pressure measurements in seven species were used to confirm that the model is a strong predictor of suction capacity in this group (Carroll et al.,

2004). Centrarchids show striking similarities in morphology and prey capture behavior to serranids, suggesting that the extension of the inferences gained from suction index to serranids is reasonable.

Statistical analysis

It has been well established that closely related species often do not represent independent data points and that phylogenetic relationships should be taken into account when comparisons are made among species (Felsenstein, 1985; Garland et al., 1992). Therefore, when analyzing our data it would be best to incorporate phylogenetic relationships to determine how kinematic traits evolve, and whether the relationships are influenced by shared ancestry. However, many of the species included in our study are not included in available phylogenetic studies, particularly species of *Pseudanthias* and *Serranus* (Baldwin and Johnson, 1993; Craig et al., 2001; McCartney et al., 2003; Craig and Hastings, 2007; Smith and Craig, 2007). We therefore chose not to incorporate any phylogenetic information, and only designate subfamily membership in scatterplots of the data. We do this because we feel incorporating poorly supported relationships would not provide more information than ignoring the relationships completely. We grouped fish into one of three subfamilies, Epinephelinae, Serraniae and Anthiinae; we chose to include the genus *Liopropoma* in Epinephelinae (Craig and Hastings, 2007).

We used a weighted Pearson's correlation coefficient, using the number of individuals per species as weights (Table 1) and the cov.wt function in R, with a two-tailed P set at 0.05 to determine: (1) whether there is a trade-off between attack speed and suction index; (2) whether there is a trade-off between mechanical advantage and lower jaw opening speed; (3) whether species that use increased attack speeds have greater excursions in cranial kinematics; (4) whether the use of jaw protrusion is associated with speed of the strike or the amount of suction a fish is capable of producing; and (5) the relationship between kinematic principal components 1–3 (PC 1–PC 3, see below) and suction index. We determined multivariate axes of between-species diversity by performing a principal component analysis (PCA) on species values of cranial kinematic parameters, and examined the relationship between suction index and each of the major kinematic PCs. The PCA, on the correlation matrix of traits, included maximum excursions during the strike (strike distance, gape, hyoid depression, jaw protrusion, cranial rotation and lower jaw rotation), time to peak gape and timings of the remaining traits relative to time to peak gape (relative

time to prey capture, peak hyoid, peak jaw protrusion, peak cranial rotation and peak lower jaw rotation; note that these relative traits were based on raw traits and not log_{10}-transformed traits); speeds were not included in this PCA because they are composite variables of timings and maximum excursions. We then used the broken-stick model to determine which PC axes to retain (Jackson, 1993). This method compares the eigenvalues of each component against eigenvalues that are obtained from dividing the total variance randomly amongst the various components following a broken-stick distribution. If the observed eigenvalues exceed the eigenvalues generated from the broken-stick distribution, then they are considered interpretable. This method revealed that the first three PCs should be retained because their eigenvalues were higher than the corresponding random broken stick components. We then correlated suction index with these three PCs to determine major axes of kinematic variation associated with the potential to generate suction. All statistical analyses were conducted using the statistical software R (v2.13). Values are presented as means ± s.e.m.

RESULTS

Our fish ranged in size from 30 mm (*Plectranthias inermis*) to 137 mm (*Diplectrum formosum*), a 4.5-fold variation in size averaging 62.25±4.56 mm (see supplementary material Table S2). Attack speed ranged from 128.33 mm s^{-1} in *Odontanthias borbonius* to 1277.88 mm s^{-1} in *P. inermis*, both belonging to Anthiinae (Table 1), approximately a 10-fold difference with a mean of 508.61±70.80 mm s^{-1} across all fishes. Attack speed was not significantly related to body size. Strike distance ranged from 2.73 mm in *O. borbonius* to 17.95 in *Epinephelus ongus*, more than a sixfold variation, with a mean of 8.29±0.75 mm. Because strike distance was significantly positively related to size, we used the residuals from a least-squares regression in final analyses. Suction index was not significantly related to size and ranged from 0.022 in *Serranus annularis* to 0.57 in *O. borbonius*, with a mean of 0.122±0.022.

We found a significant negative relationship between suction index and both attack speed (r=–0.446, P=0.013) and residual strike distance (r=–0.436, P=0.016), and a strong positive correlation between attack speed and residual strike distance (r=0.887, P<0.0001; Fig. 2). This suggests a potential trade-off in predation strategies: species that strike from farther distances use faster attack speeds and have a low potential for suction, whereas those that strike from close distances use slower attack speeds, but have a high potential for suction (Fig. 2). We did not find a relationship between attack speed and residual mouth opening speed (r=0.08, P=0.66).

We found no relationship between jaw-opening mechanical advantage and speed of jaw depression during mouth opening (Fig. 3). Species that had a high mechanical advantage for the lower jaw opening lever did not have decreased speeds when speeds are taken as the residuals from log_{10} standard length (r=0.27, P=0.29; Fig. 3A) or log_{10} lower jaw length (r=0.22, P=0.41; Fig. 3B). Furthermore, although there is a significant relationship between maximum rotation of the lower jaw and lower jaw rotation speed (r=0.54, P=0.002), including this relationship does not alter the results. When residual lower jaw rotation speed is taken from a multiple regression with log_{10} standard length and log_{10} maximum lower jaw rotation, it is not significantly related to mechanical advantage (r=0.26, P=0.17). Additionally, when residual lower jaw rotation speed is obtained from a regression with maximum lower jaw rotation only, there is no significant relationship with mechanical advantage (r=–0.12, P=0.52). Lastly, we did not find a relationship between attack speed and speed of the lower jaw depression when
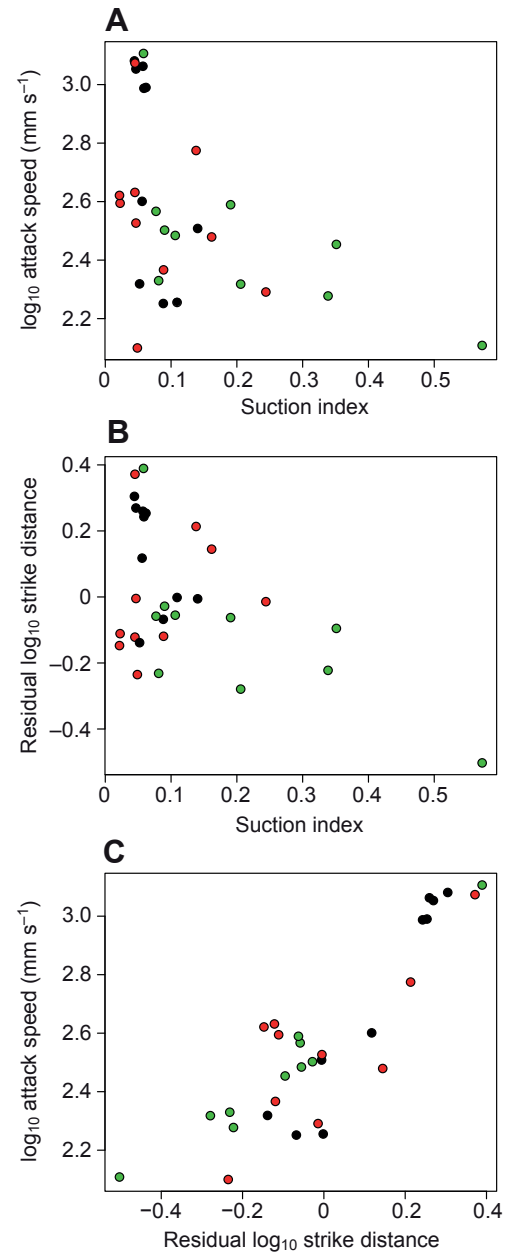
Fig. 2. Relationship between (A) suction index and log_{10} attack speed, (B) suction index and residual log_{10} strike distance and (C) residual log_{10} strike distance and log_{10} attack speed. Species that strike from a farther distance have increased attack speed and low suction index. Conversely, species that strike from close distances and use slower speeds exhibit a wide range of suction indices. Points are colored by subfamily: Epinephelinae in black, Serraninae in red and Anthiinae in green.

residual lower jaw rotation speed was taken from regressions with standard length (r=0.12, P=0.54), length of the lower jaw (r=0.26, P=0.16), maximum lower jaw rotation (r=–0.23, P=0.22) or standard length and maximum lower jaw rotation (r=–0.31, P=0.09).

We also found that species that use higher attack speeds have greater excursions of all cranial kinematics (question 3; Fig. 4). Species that use high attack velocities have larger gapes (r=0.572, P=0.001; Fig. 4A), greater depression of the hyoid (r=0.585, P=0.0007; Fig. 4B) and more rotation of the cranium (r=0.771, P<0.0001; Fig. 4C) and lower jaw (r=0.702, P<0.0001; Fig. 4D)
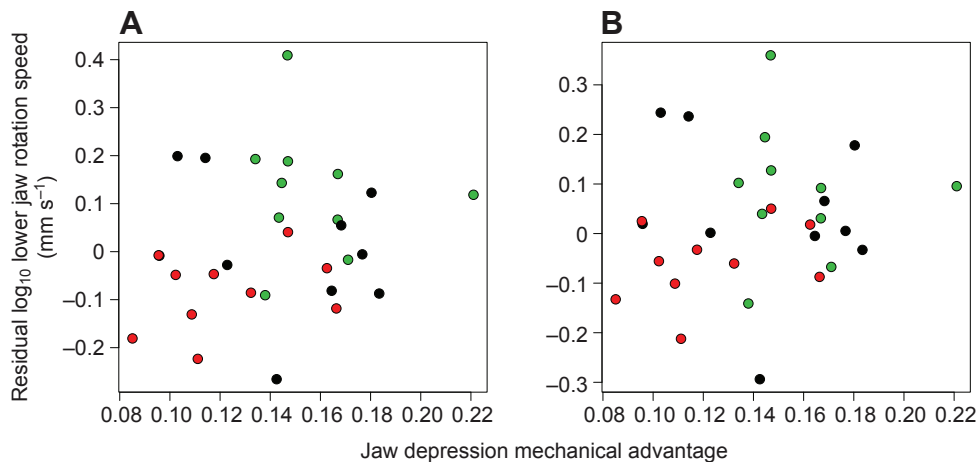
Fig. 3. The mechanical advantage of the lower jaw opening lever does not show a trade-off with residual lower jaw opening speed, when residuals are obtained from a regression with either (A) $\log_{10}$ standard length ($r=0.201$, $P=0.286$) or (B) when lower jaw rotation speed residuals are obtained from a regression with $\log_{10}$ lower jaw length ($r=0.155$, $P=0.414$). Points are colored by subfamily: Epinephelinae in black, Serraninae in red and Anthiinae in green.

during a strike. Furthermore, species that use faster attack speeds also have increased jaw protrusions ($r=0.426$, $P=0.019$). Therefore, in relation to question 4, jaw protrusion is associated with the speed of attack in this group of fish (Fig. 5A). However, there was no relationship between attack speed and jaw protrusion speed ($r=0.23$, $P=0.21$; Fig. 5B), and no relationship between suction index and maximum jaw protrusion ($r=0.07$, $P=0.73$; Fig. 5C) or jaw protrusion speed ($r=0.16$, $P=0.41$). Finally, although we found a significant positive correlation between attack speed and maximum gape during a strike, there was no significant relationship between attack speed and residual $\log_{10}$ mouth diameter measured horizontally on cleared and stained

specimens, and used in suction index calculations ($r=0.12$, $P=0.52$; Fig. 6A).

Finally, we found that the morphological potential to generate suction was significantly related to two of the three PCs retained by the broken stick model (Table 2). Suction index was significantly positively correlated with PC 1, where high values of PC 1 are characterized by species with short strike distances, smaller gapes, less hyoid depression, less rotation of the cranium and lower jaw, a longer relative time to peak cranial rotation and slower time to peak gape. Therefore, species that have a greater potential for suction, have less movement of cranial kinematics and take longer to reach peak gape and head angles. Suction index was not related to PC 2, which
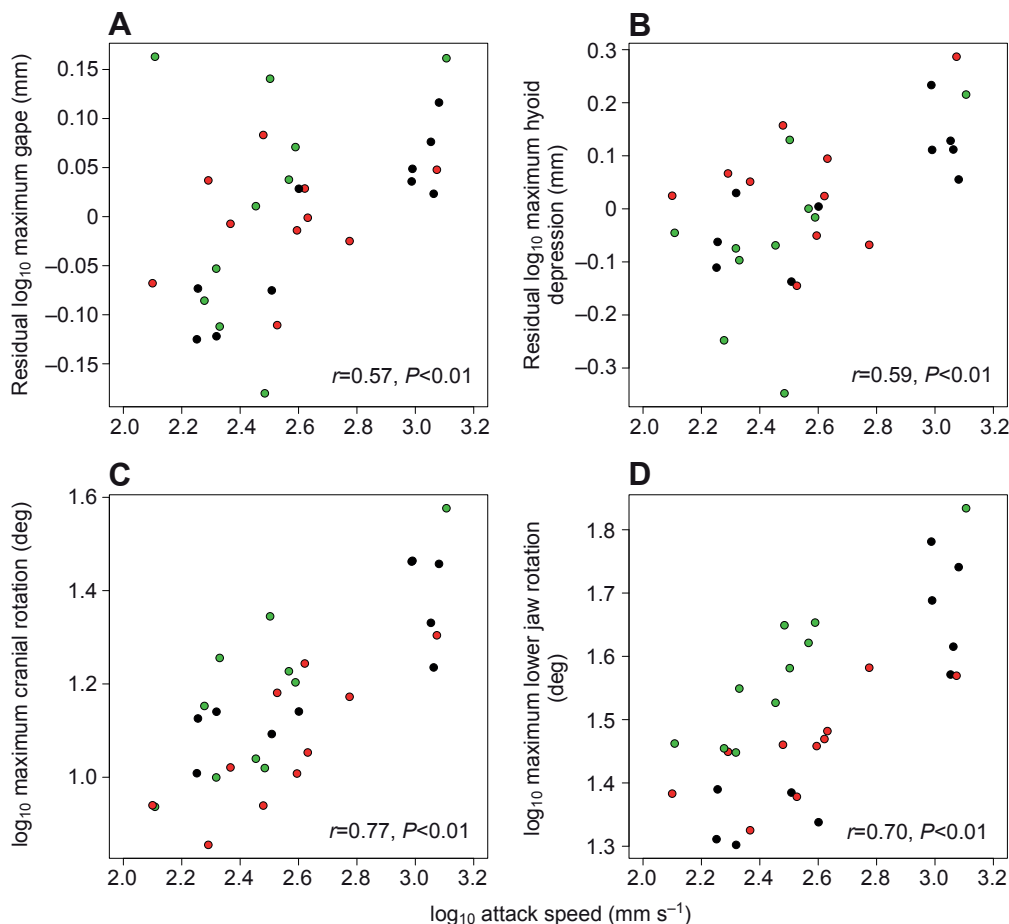

Fig. 4. Species that use higher attack speed exhibit greater excursions of cranial kinematics – (A) residual $\log_{10}$ maximum gape, (B) residual $\log_{10}$ maximum hyoid depression, (C) $\log_{10}$ cranial rotation and (D) $\log_{10}$ lower jaw rotation – potentially to compensate for a decrease in accuracy. Points are colored by subfamily: Epinephelinae in black, Serraninae in red and Anthiinae in green. Note that with *Odontanthias borbonius* removed, the correlation coefficient for attack speed/gape increases to $r=0.65$.
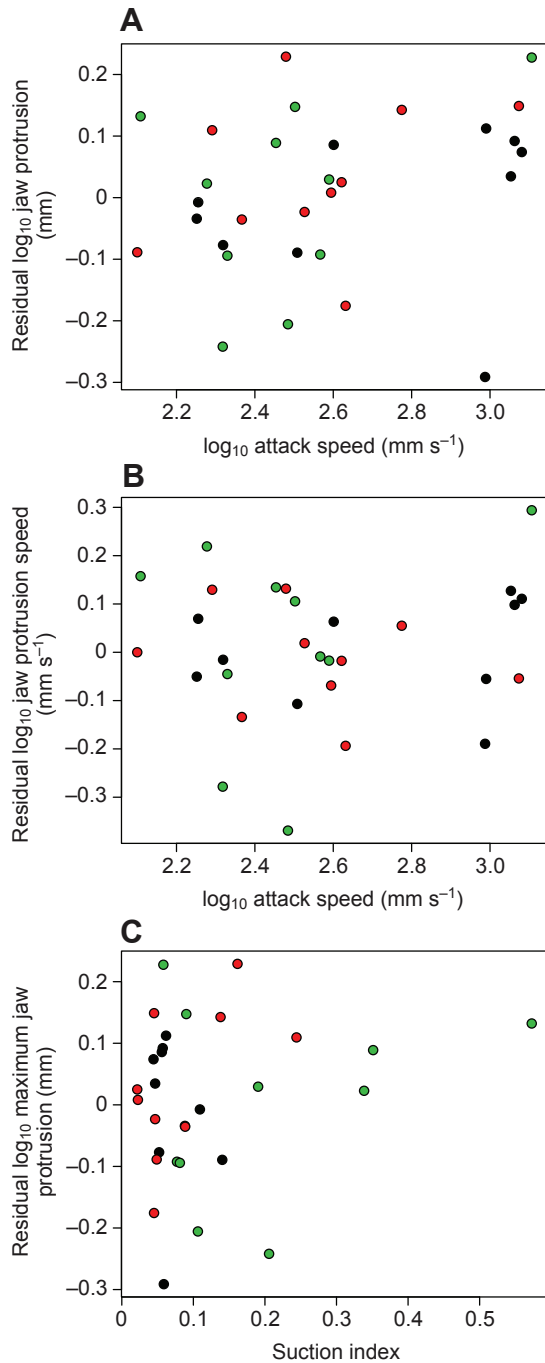
Fig. 5. Among the serranid species in the present study, the use of jaw protrusion was associated with attack speed, as evidenced by a positive correlation between $\log_{10}$ attack speed and residual $\log_{10}$ maximum jaw protrusion (A; r=0.426, P=0.0019). However, jaw protrusion speed was not related to attack speed (B; r=0.23, P=0.21), and maximum jaw protrusion was not related to suction index (C; r=0.07, P=0.73). Points are colored by subfamily: Epinephelinae in black, Serraninae in red and Anthiinae in green.

Fig. 6. The trade-off between suction index and attack speed is not due to high-speed attackers having larger mouths (A; r=0.123, P=0.517), or species with high suction index having smaller mouths (B; r=−0.207, P=0.272). However, there is a significant relationship between suction index and residual $\log_{10}$ epaxial height (C; r=0.824, P<0.0001), suggesting the trade-off between suction index and attack speed is due to the elongate body form of high-speed attackers limiting hypertrofication of the epaxial muscle. Points are colored by subfamily: Epinephelinae in black, Serraninae in red and Anthiinae in green.

is characterized primarily by relative time to prey capture and relative timing of peak lower jaw rotation. Finally, suction index was significantly positively correlated with PC 3. Low values on PC 3 are characterized by species that tend to have high suction indices and relatively large gapes, and reach peak hyoid depression after peak gape. This axis is mainly characterized by the species *O. borbonius*,
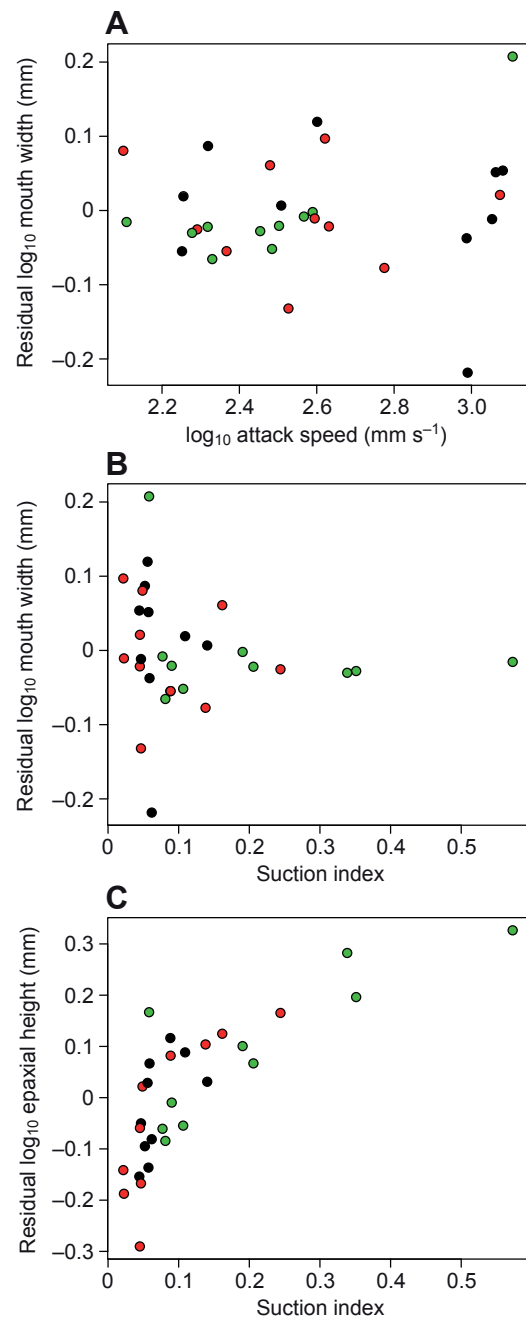
the species with the highest suction index, which also has a relatively large gape (Anthiinae data point in upper left corner of Fig. 4A).

DISCUSSION
Using a large detailed data set on an ecologically diverse group of fishes, we found that evolution has produced considerable diversity

Table 2. Principal component analysis on maximum excursions, time to peak gape and timings relative to peak gape

Trait	PC 1	PC 2	PC 3
Strike distance[a]	−0.413	0.200	0.048
Maximum gape[a]	−0.315	−0.269	−0.405
Time to peak gape[a]	−0.307	−0.248	0.297
Maximum hyoid[a]	−0.389	−0.184	−0.081
Maximum jaw protrusion[a]	−0.229	−0.279	−0.200
Maximum head angle[b]	−0.323	0.294	−0.251
Maximum lower jaw rotation[b]	−0.307	0.272	−0.326
Relative time to peak hyoid depression	0.132	−0.250	−0.554
Relative time to prey capture	0.000	0.534	−0.109
Relative time to peak jaw protrusion	0.282	−0.087	−0.349
Relative time to peak head angle	0.363	−0.033	−0.251
Relative time to peak lower jaw rotation	0.077	0.444	−0.163
Variance (%)	36.17	20.60	14.71
Cumulative variance	36.17	56.78	71.49
Pearson's correlation with suction index	$r=0.423, P=0.020$	$r=0.274, P=0.147$	$r=-0.383, P=0.037$

A broken stick model retained the first three principal components, which explain 71.5% of the variation. Suction index is significantly correlated to all three independent PC axes.

[a]Traits are residual $\log_{10}$ values from a regression with $\log_{10}$ standard length.

[b]Traits are $\log_{10}$ values.

in strike kinematics and suction-feeding capacity. Our results lend support to the notion that trade-offs may be less of a constraint than once thought in the diversification of complex functional systems, such as suction feeding (Holzman et al., 2011). Below, we explore the results from each of the five expected principles in more detail.

Suction index and attack speed

The continuum that spans strikes in which suction is relied upon to draw prey into the mouth and strikes in which prey are overtaken by a fast-swimming predator has been a major starting point in discussions of the diversity of fish prey-capture strategies (Norton and Brainerd, 1993; Gibb, 1997; Wainwright et al., 2001; Porter and Motta, 2004; Gibb and Ferry-Graham, 2005; Higham et al., 2005; Flammang et al., 2009; Kane and Higham, 2011). Liem (Liem, 1980) initially identified three general strategies, 'ram' feeders that use high attack speed, suction feeders and manipulators. Many other investigators have noted an apparent negative association between features that enhance suction feeding and features associated with a fast-swimming attack (Lauder and Liem, 1981; Van Leeuwen, 1984), while others suggest that fast-swimming attackers may also use considerable suction (Muller and Osse, 1984; Van Damme and Aerts, 1997). It is therefore not clear whether there should be a trade-off between suction and pursuit. Among the serranids, the relationship between the capacity to generate suction and the speed used during attack was more complex than a simple trade-off. Although the morphological capacity to generate suction pressure was negatively associated with attack speed, confirming the classic relationship, our large sample of species allowed us to see that the relationship only occurred in one of the three subfamilies, Anthiinae, and was considerably more complex than predicted (Fig. 2). Specifically, the diversity of suction index is strongly related to attack speed. No species that strike at high swimming speeds have a high suction index (Fig. 2): all of the species with the highest attack speeds have very low potential to generate suction pressure. This contrasts markedly with extensive diversity in suction index among species that used slow attack speeds (Fig. 2). The absence of fast-attacking species with strong suction capacity was also noted in a small sample of seven cichlid species (Wainwright et al., 2001). The absence of species with the morphological potential to generate strong suction pressure suggests that previous predictions that

suction generation in high-speed attackers would be similar to slower attackers (Van Damme and Aerts, 1997) will need to be reconsidered. The complete absence of species capable of strong suction among the high-speed attackers is one of the strongest patterns in our data set and suggests a basic incompatibility between design for strong suction and a fast-swimming attack.

This relationship suggests that species with a high capacity for suction do not attack at high speeds, whereas those with low morphological potential for suction attack at a range of speeds. One possible cause of this pattern is that the low range of suction indices among high-speed attackers reflects a functional constraint. Perhaps the poor accuracy thought to occur in high-speed attacks is incompatible with the small mouth that should characterize species with a high suction index? However, among our sample of serranids there is not a significant relationship between attack speed and residual $\log_{10}$ mouth diameter measured on cleared and stained specimens ($r=0.123$, $P=0.517$; Fig. 6A), or between suction index and mouth diameter ($r=-0.207$, $P=0.272$; Fig. 6B). Nevertheless, species that struck at higher speeds exhibited larger gapes (as obtained from videos) (Fig. 4A), suggesting that the amount of suction generated may be modulated with attack speed (Nemeth, 1997; Ferry-Graham et al., 2001; Van Wassenbergh et al., 2006; Tran et al., 2010; Van Wassenbergh and De Rechter, 2011; Arena et al., 2012). A second possibility is that the elongate body form of high-speed attackers may preclude the hypertrofication of epaxial muscle attaching to the back of the neurocranium, as seen in species with high suction indices, which seems to be the case in our sample of serranids. There is a significant positive correlation between suction index and residual $\log_{10}$ epaxial height ($r=0.824$, $P<0.0001$; Fig. 6C), and a significant negative correlation between attack speed and residual $\log_{10}$ epaxial height ($r=-0.427$, $P=0.019$). Whatever the cause of the pattern, the implication is that the continuum between the use of attack swimming and suction to capture prey is not a simple trade-off. Species that attack relatively slowly show the full range of morphological potential for suction, whereas high-speed attacks are limited to species with poor suction capacity.

Trade-offs in lever systems

One of the most commonly referenced principals of teleost skull functional morphology is that the mechanical advantage of levers

reflects a trade-off between force and velocity transmission. This expectation is based on the assumption that the input velocity to a lever is held constant because under these conditions the basic trade-off in lever systems occurs. However, recent work has pointed out that the effect of lever mechanics on muscular input velocity is often considerable and the expected trade-off may not exist under many reasonable conditions (Arnold et al., 2011; McHenry and Summers, 2011; McHenry, 2011). Lever configuration influences the resistance experienced by the input muscle, which may result in different contractile speeds with the muscle experiencing the same level of neural excitation. Serranids showed no suggestion of a relationship between lower jaw opening lever mechanical advantage and the speed of rotation of the lower jaw during mouth opening (Fig. 3). This is a particularly interesting result because previous studies of fish skull levers have repeatedly found a correlation between mechanical advantage and ecological traits, such as preferred prey (Wainwright and Bellwood, 2002; Wainwright et al., 2004; Case et al., 2008; Cooper and Westneat, 2009), that are consistent with traditional interpretations of lever trade-offs. For example, species of Labridae that bite and remove attached molluscs from rocky walls have a relatively high jaw closing mechanical advantage whereas piscivorous and zooplanktivorous species have a lower mechanical advantage in the same lever (Wainwright et al., 2004; Bellwood et al., 2006). Nevertheless, to our knowledge these are the first comparative data from fish feeding mechanisms that test for the expected relationship between lever mechanics and speed of movement across the joint. As the assumption of a constant input velocity in this system across species is clearly violated, we suggest that the muscles and other linkage systems that transmit force and velocity through this lever may be diverse and the effect of loading on shortening speed is difficult to predict.

Mandible depression in serranids and other teleosts also shows complexity proximal to the attachment of the interopercular-mandibular ligament on the retroarticular process of the mandible. This system is not characterized by a muscle that inserts directly upon the retrorarticular process. Instead, the largest input contribution is thought to derive from hypaxial muscle and sternohyoideus contractions that retract the hyoid bar (Carroll and Wainwright, 2006). The hyoid bar is connected by a ligament to the interopercular bone that transmits tension to the interopercular-mandibular ligament and thus to the mandible. In addition, the protractor hyoideus muscle inserts on the mandibular anteriorly, crosses the jaw joint and originates on the hyoid bar. Under very restricted, species-specific conditions, this muscle, though small in cross-sectional area, has a line of action that allows it to depress the mandible. Also, the opercular four-bar linkage transmits a small fraction of the force and motion input by the levator opercula muscle to the interopercular-mandibular ligament and contributes some to depression. We suggest that neither of these last two mechanisms makes a major contribution to lower jaw depression during the powerful expansion of the mouth and buccal cavity during suction feeding in serranids because both mechanisms are mechanically weak relative to the ventral coupling to the hypaxial muscles. Further, it is unclear whether the opercular four-bar transmits movement in the way that it was originally described (Westneat, 1994). Even if some of these potential contributors to lower-jaw depression have little effect, it is clear that complexity in the systems that provide input to the lower jaw lever offer numerous opportunities for lineage-specific modifications that could contribute to diversity in lower jaw depression speed during prey capture. Whatever the ultimate explanation, the key point from our result is that the mechanical advantage of the jaw-depression lever in serranids cannot be used as a morphological indicator of the speed of jaw opening.

Attack speed and cranial kinematics

A potential consequence of relying on increased speeds during an attack is a decrease in accuracy of the strike (Higham et al., 2006; Higham, 2007; Higham et al., 2007). Among centrarchid fishes, largemouth bass exhibit decreased accuracy and use higher attack speeds during the strike than bluegill, which have increased accuracy and use slower attack speeds (Higham et al., 2006). Although it is risky to make generalizations from a two-species comparison, the results suggest that species that use higher attack speeds may exhibit a decrease in accuracy. However, fast-attacking fish may compensate by ingesting a larger volume of water to ensure prey capture. During a suction-feeding event, there is coordinated movement of the musculoskeletal system to rapidly expand the buccal cavity (Lauder, 1980; Wainwright et al., 2007). Species that use high attack speeds may exhibit an increase in any one or a combination of cranial kinematic traits to increase the amount of water drawn into the buccal cavity (Porter and Motta, 2004; Wintzer and Motta, 2005; Tran et al., 2010; Kane and Higham, 2011). For example, cichlid species that use higher attack speeds also exhibit increased gapes (Higham et al., 2006). However, few studies have looked at other cranial excursions, such as cranial and lower jaw rotation and hyoid depression, in relation to attack speeds used during a strike. We found that serranid species using faster attack speeds exhibited significantly larger values of peak gapes, similar to previous studies. We also found that fast-attacking species also exhibited greater rotation of the cranium and lower jaw and greater depression of the hyoid (Fig. 4), supporting the hypothesis that fish relying on faster speeds ingest more water to either compensate for a decrease in accuracy or gain some other advantage of high-volume suction feeding (Carroll and Wainwright, 2011). Interestingly, there was no relationship between attack speed and the anatomically measured mouth diameter of the same specimens (Fig. 6A), suggesting that the tendency for fast-attacking species to expand their mouth to a greater degree is involved in the pattern.

Similar kinematic results have been found at the intraspecific level in fish. Tran et al. (Tran et al., 2010) found that magnitudes of gape, cranial elevation, lower jaw rotation and hyoid displacement all increased with increasing attack speed within individuals of Indo-Pacific tarpon (*Megalops cyprinoides*), and also found a significant positive correlation between attack speed and strike distance. Therefore, a predator may modulate its strike depending on when the strike is initiated and the speed of the attack. The positive relationship between attack speed and cranial kinematics and the lack of a relationship with anatomical mouth diameter may therefore be due to behavioral differences of the predators. This potential behavioral variation may also partly explain why some species with a low suction capacity use slower speeds during a strike (Fig. 2).

Jaw protrusion as an alternative to attack speed

Upper jaw protrusion results from anterior sliding of the premaxilla, and both enhances the suction forces and helps close the distance to the prey item (Motta, 1984; Hulsey and García de León, 2005; Ferry-Graham et al., 2008; Holzman et al., 2008c; Hulsey et al., 2010). Although some authors have noted considerable jaw protrusion in fish that attack at high speed (Lauder and Liem, 1981), and others have noted that jaw protrusion works synergistically with swimming to move the mouth quickly toward the prey (Holzman et al., 2012a), jaw protrusion has also been viewed as an alternative to fast-attack swimming to minimize the

predator–prey distance (Norton and Brainerd, 1993). One therefore might expect a negative relationship between attack speed and maximum jaw protrusion or jaw protrusion speed. Similarly, we might expect a positive relationship between suction index and maximum jaw protrusion, if jaw protrusion varies in relation to predation strategy. We found no support for these hypotheses. Instead, we found a weak but significant positive relationship between attack speed and the amount of jaw protrusion (Fig. 5A), indicating that attack speed and jaw protrusion are used synergistically in some species to quickly approach the prey. However, we found no relationship between attack speed and jaw protrusion speed (Fig. 5B), or between suction index and maximum jaw protrusion (Fig. 5C), indicating that different combinations of jaw protrusion and suction capacity are used across serranid species. Jaw protrusion was not restricted to species that have a high morphological potential to generate suction pressure, and varied approximately sevenfold among serranid species (1.1–7.5 mm). Furthermore, jaw protrusion ranged from 3.14 to 10.65% of standard length, similar to the variability found in other fish groups, such as cichlids (Hulsey and García de León, 2005), but less than species that exhibit extreme jaw protrusion [e.g. *Luciocephalus pulcher* (Lauder and Liem, 1981), *Petenia splendida* (Waltzek and Wainwright, 2003; Hulsey and García de León, 2005) and *Epibulus insidiator* (Westneat and Wainwright, 1989)].

Kinematic variation in relation to suction index

How are the kinematics of a strike related to the capacity to generate suction pressure? We found three PCs that each accounted for greater variation than would be expected by chance (Table 2). Thus these represent three independent, uncorrelated axes of kinematic variation among species of serranids. Suction index was correlated with two of these three PCs (PC 1 and PC 3; Table 2), indicating that although these PCs are uncorrelated with each other, they are both moderately related to the capacity to generate suction pressure. The first PC indicated a trend for species with short attack distances and smaller kinematic excursions to show a timing pattern where kinematic events are less synchronous than in fast-attacking species with large excursions. The second PC captured a trend for species with delayed time of peak lower jaw depression and prey capture to strike from farther away, and was not related to the capacity to generate suction. The third PC was dominated by a trade-off between peak gape distance and the timing of peak gape expansion. Although studies have examined the effects of scaling on suction index (Holzman et al., 2008a) and diversification of morphological components of suction index (Collar and Wainwright, 2006), no studies have looked at how the morphological potential to generate suction relates to the kinematics of the cranium during a strike. Future studies should continue to incorporate morphological measurements with kinematic data to determine how the traits are related and how species that are considered to be strong suction feeders perform during a suction-feeding event.

CONCLUSIONS

The considerable diversity found among 30 species of serranids reveals complexity in the ram–suction continuum. Although species that use fast attack speeds had very low morphological capacity to generate suction pressure, species that attack at slower speeds exhibited the full range of suction index values. This raises the possibility that the morphology of fish for high-speed attacks is incompatible with specialization for strong suction feeding, whereas the morphology for low-speed attacks is permissive. Swift-attacking species also exhibited greater excursions of cranial movements, potentially to compensate for the decrease in accuracy during faster strikes by increasing the volume of water that is drawn through the buccal cavity during the strike (Fig. 4, Table 2). Furthermore, we found a positive relationship between attack speed and maximum jaw protrusion (Fig. 5A), suggesting that high-speed attackers may have increased jaw protrusion to help minimize the predator–prey distance. However, we found no relationship between suction index and the amount of jaw protrusion (Fig. 5B), further suggesting that protrusion is a versatile feature of the feeding mechanism across species that vary in their capacity to generate suction. Finally, we found no evidence of the often-assumed trade-off between the mechanical advantage of the lower jaw opening lever and the speed of jaw depression (Fig. 3). The results from this study show that large comparative data sets can be used to reveal previously unknown patterns in the distribution of fish species in functional morphospace.

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